The Comparative Morphology and Evolution of the Molluscan Mantle Edge

BY

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(13 Text figures)

INTRODUCTION

In a recent evaluation of the probable course of molluscan evolution Stasek concurred with Lang (1896) in viewing the phylum as descended from free-living flatworms that were dorsally covered by a cuticle (Stasek, 1972). This cuticle was the precursor of the calcified shell characteristic of the higher Mollusca and, together with trends toward increase in size, was the evolutionary factor responsible for the subsequent appearance of most of the other anatomical features that distinguish the group as a phylum.

The rationale underlying that idea is that the cuticle, and its later elaboration as a shell, developed in relation to protection, but inhibited locomotion and diffusion of respiratory gases. The open circulatory system with hemocoelic sinuses, pumping heart, "coelom," and gills all evolved in relation to improved respiratory function. It was in relation to augmented protection and to increased facility of locomotion that the sides of the body and cuticle became extended as eaves beyond the body proper. These lobes functionally released the body from the edges of the cuticle or shell, thereby increasing freedom of movement, especially turning of the organisms. The mantle lobes, mantle cavity, and foot, all basic qualities of the molluscan framework, are the topographic results of this development.

The dorso-ventral muscles of the antecedents became the pedal retractor muscles of the mollusks, with insertions achieved upon the shell by modification of the epithelium at the ends of the muscles adjacent to the shell surface. Four stages in the evolution of the molluscan framework are illustrated in Figure 1. Further development of this view, its qualifications, and references are included elsewhere (Stasek, 1972). With the emergence of these ideas it became apparent that the region lying immediately adjacent to the edges of the cuticle, the future mantle margin, required special phylogenetic consideration. The present paper is addressed to that topic,

COMPARATIVE MORPHOLOGY AND INFERRED EVOLUTION OF THE MANTLE MARGIN

Synopsis: As retrospectively inferred from conditions in the 7 extant classes, the major stages in the evolution of the mantle margin were probably as follows. The initial cuticle of the predecessors was added to peripherally and in thickness as growth took place (Figure 1B, c). Spicules of calcium carbonate may have been laid down in the cuticle at intermediate stages of evolution, but later deposition of calcareous layers formed a shell and lifted the original cuticle above the secretory epithelium (Figure 1D, p). During this transition the sites of production of the now thin uncalcified portion (periostracum) became limited to a submarginal zone around the periphery of the shell. This zone was probably sunken into a shallow trough, the incipient periostracal groove (Figures 1C, 1D, pg). Surrounding the edge of the zone of periostracal secretion there extended a retractible ring of tissue, the mantle rim (Figure 1C, mr), with an accessory fold bearing mucous glands located submarginally on its undersurface (Figure 1C, af). The mantle rim, together with the accessory fold and the mantle immediately proximal to the periostracal groove, was the precursor of the mantle margin in all the higher classes. These events took place during Precambrian times, but descendants of various early intermediate forms and side branches are still with us.

The Subphylum Aculifera: The most significant of these intermediate forms are now placed together in a class, the wormlike Aplacophora (Subphylum Aculifera),

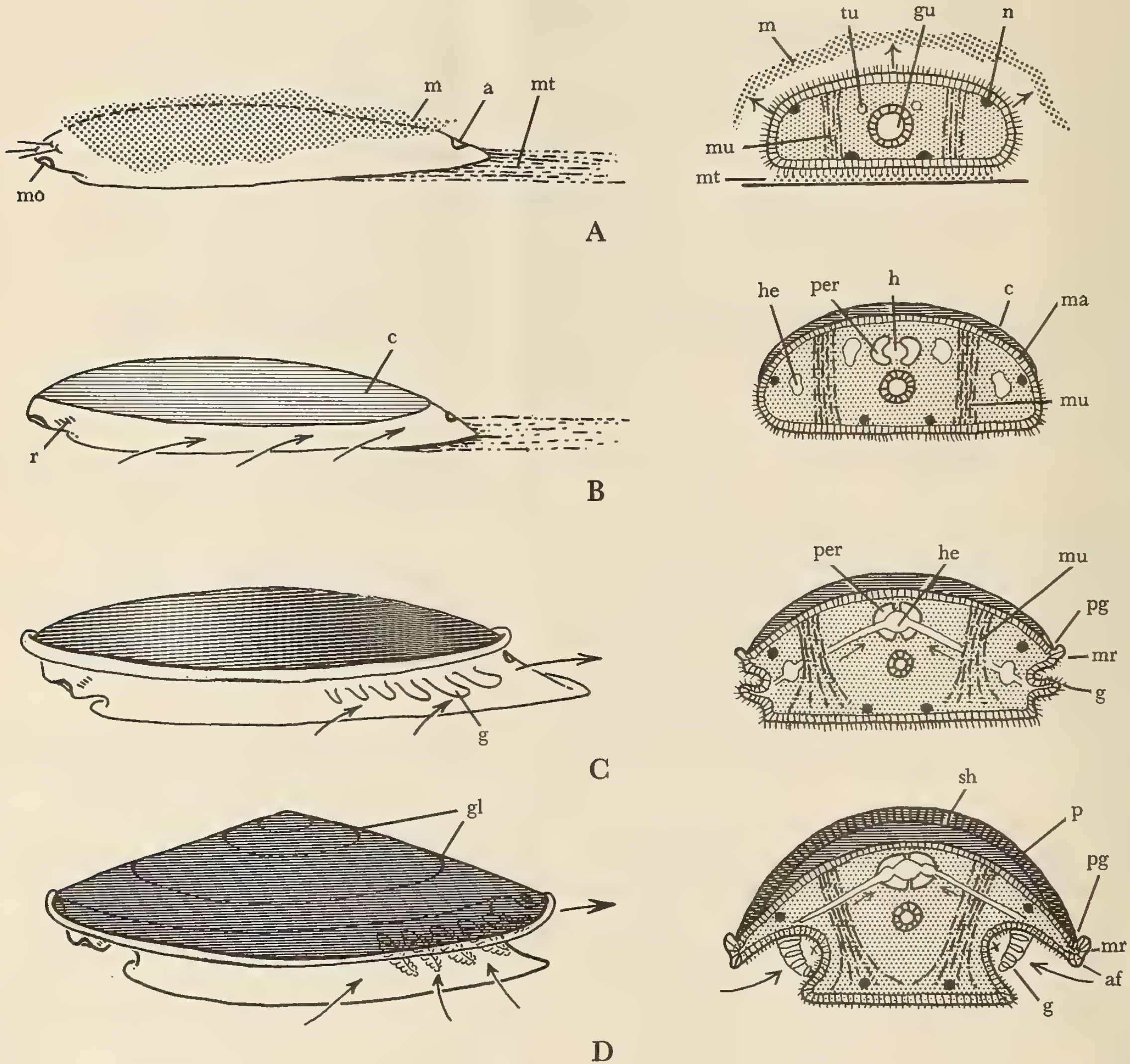

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Figure 1

Four stages in the evolution of the molluscan framework from flatworm-like stock, all shown in lateral and cross-sectional aspects

A. Proposed ancestral form with complete gut and ability to secrete mucus as a protective measure and as a locomotory track.

B. Transitional stage with radula and cuticle. The cuticle is thin at the periphery where marginal growth takes place, but because the cuticle is retained throughout life, it becomes thicker in the older portions.

C. Transitional molluscan stage with an incipient mantle cavity. The cuticle arises from a shallow periostracal groove beyond which the mantle rim extends.

D. Advanced molluscan stage with calcified layers laid down under the uncalcified periostracum. The mantle rim is still simple.

a – anus; af – accessory fold of mantle associated with production of mucus; c – cuticle; g – ciliated gill; gl – growth lines; h – heart; he – unlined blood spaces; m – protective mucous coat; ma – mantle; mo – mouth; mr – mantle rim; mt – mucous track; mu – dorso-ventral muscles from which pedal muscles were derived; p – thin periostracum derived from the original cuticular layer; per – pericardium; pg – periostracal groove; r – radula; sh – shelly layers of calcified cuticle; tu – gonoducal tubules form the heart and pericardium in later stages; x – site of excurrent chamber of respiratory current; arrows in B - D indicate respiratory flow of water. From Stasek, 1972, © Academic Press, Inc.

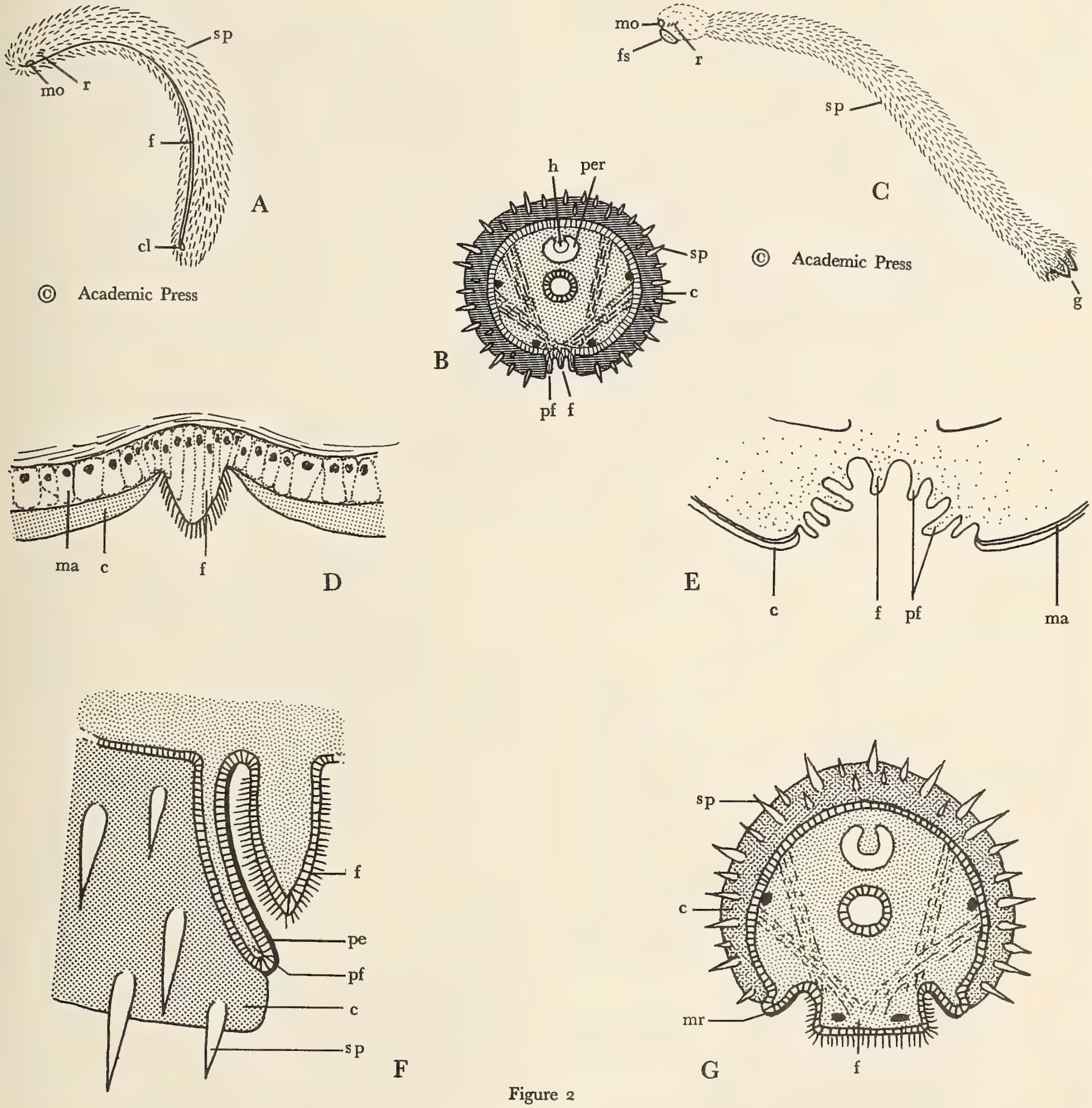


Figure 2

Aplacophora

A. Form with rudimentary foot and spiculous cuticle. B. Cross-section of A showing enrollment of heavy cuticle. To either side of the foot is a single pedal fold held to be homologous with the mantle rim of other mollusks. C. Form without a foot, the body being completely encircled by cuticle. D. Cross-section through foot and edges of the cuticle in a form without pedal folds. E. Cross-section through ventral region of a species with 4 pedal folds on either side of the foot. F. Cross-section of a species with one cuticular pedal fold on either side of the foot; enlarged from B. above. G. Cross-section through entire body of a hypothetical form antecedent to the more complicated enrolled Aplacophora shown in B.

c – cuticle; cl – cloaca; f – foot; fs – foot shield; g – gill; h – heart; ma – mantle; mo – mouth; mr – mantle rim; pe – pellicle; per – pericardium; pf – pedal folds; r – radula; sp – spicules. A, B, C from Stasek, 1972, © Academic Press, Inc. D, E, F suggested by Hyman, 1967, figs. 6 and 7.

characterized not by a shell but by a spiculose cuticle that nearly or entirely encloses the body (Figures 2A, 2B, 2C). Salvini-Plawen (1969) gave class rank to each of the two body types.

In a simple instance (Figure 2D) the arrangement of the cuticular border resembles that proposed for one of the hypothetical intermediate ancestral forms (Figure 1B), except for cross-sectional proportional differences brought about by enrollment of the cuticle. Increase in diameter of the body is thought to take place by growth of the mantle above the medial edges of the cuticle (Beedham & Trueman, 1968), recalling the site of the "generative zone" of the mantle discussed below in relation to higher forms (p. 14). In these aplacophorans respiratory gas exchange probably takes place posteriorly through the unfolded walls of an enlarged cloaca (Figure 1A, cl) and through the epithelium of the foot (Leloup, 1950).

More elaborate conditions are found in those aplacophorans bearing one or more pedal folds lateral to the foot (Figures 2E, 2F, pf). In a common instance (Figure 2F) such folding gives rise to a condition reminiscent of the mantle rim of more advanced molluscan types. Folds or finger-like projections from the walls of the cloaca, as well as the pedal folds, account for respiratory gas exchange in these forms. Although any suggestion of homology, such as that made elsewhere (Stasek, 1972: 18), is strictly provisional, the anatomical similarities of these regions in aplacophorans and in the higher classes do exist, and a hypothetical form with a mantle rim is postulated as having led to more enrolled aplacophorans (Figure 2G). One may note in Figure 2F that the inner surface of the pedal fold is covered by a thin cuticular layer, the pellicle (pe). This secretion is aspiculous and its general nature differs considerably from that of the spiculose cuticle covering the body proper. The epithelia comprising either side of the pedal fold also differ: that secreting the pellicle resembles the surface of the foot, while that adjacent to the spiculose cuticle recalls the general cuticle-secreting surface of the body (Fischer-Piette & Franc, 1960: 1662).

Those Aplacophora that are completely encircled by a cuticle respire through a pair of highly folded gills resembling, and perhaps homologous with, the ctenidia of the higher mollusks (Figure 2C, g).

The Subphylum Placophora: A later, more highly evolved side branch of the Mollusca comprises the chitons, class Polyplacophora (subphylum Placophora), which have maintained the elongate body and broad foot of unrecorded ancestral forms (Figure 3A). Antecedents to this and to all succeeding classes developed the ability to regulate the deposition of calcium carbonate to form solid layers. The chitons are characterized by a shell of 8 overlapping plates, the jointing of which permits anteroposterior flexibility.

More clearly than in the proposed primitive condition, the mantle margin of the Polyplacophora is divisible into 3 regions. First there is a small fold (Figure 3B, of) medial to the periostracal groove and concerned with secretion of the shell. Second, there is the large mantle rim (Figure 3B, mr) lateral to the periostracal groove. And third, there is a swollen accessory fold bearing mucous glands on the undersurface of the mantle (Figure 3B, if; Beedham & Trueman, 1967: 221). The point to be stressed here is that the mantle rim of the ancestral mollusks was hypertrophied, forming the girdle in the Polyplacophora. This structure assures close protective contact with the substratum, except where raised to allow entrance and exit of the respiratory water currents. The surface of the girdle is exposed to the sea, but is covered by a thickened and generally spiculose cuticle (Figure 3B, c), which can be regarded as at least partially homologous with the pellicle that covers the single pedal fold of many aplacophorans.

A cuboidal or low columnar epithelium forms the general mantle surface under the shell plates (Hyman, 1967: 75). The epithelium of the girdle, in contrast, is of a high columnar nature, and the cells are peculiarly grouped into packets (Figure 3B, pa), with spaces often intervening between them. The packets of cells secrete the spicules, which project into or through the overlying

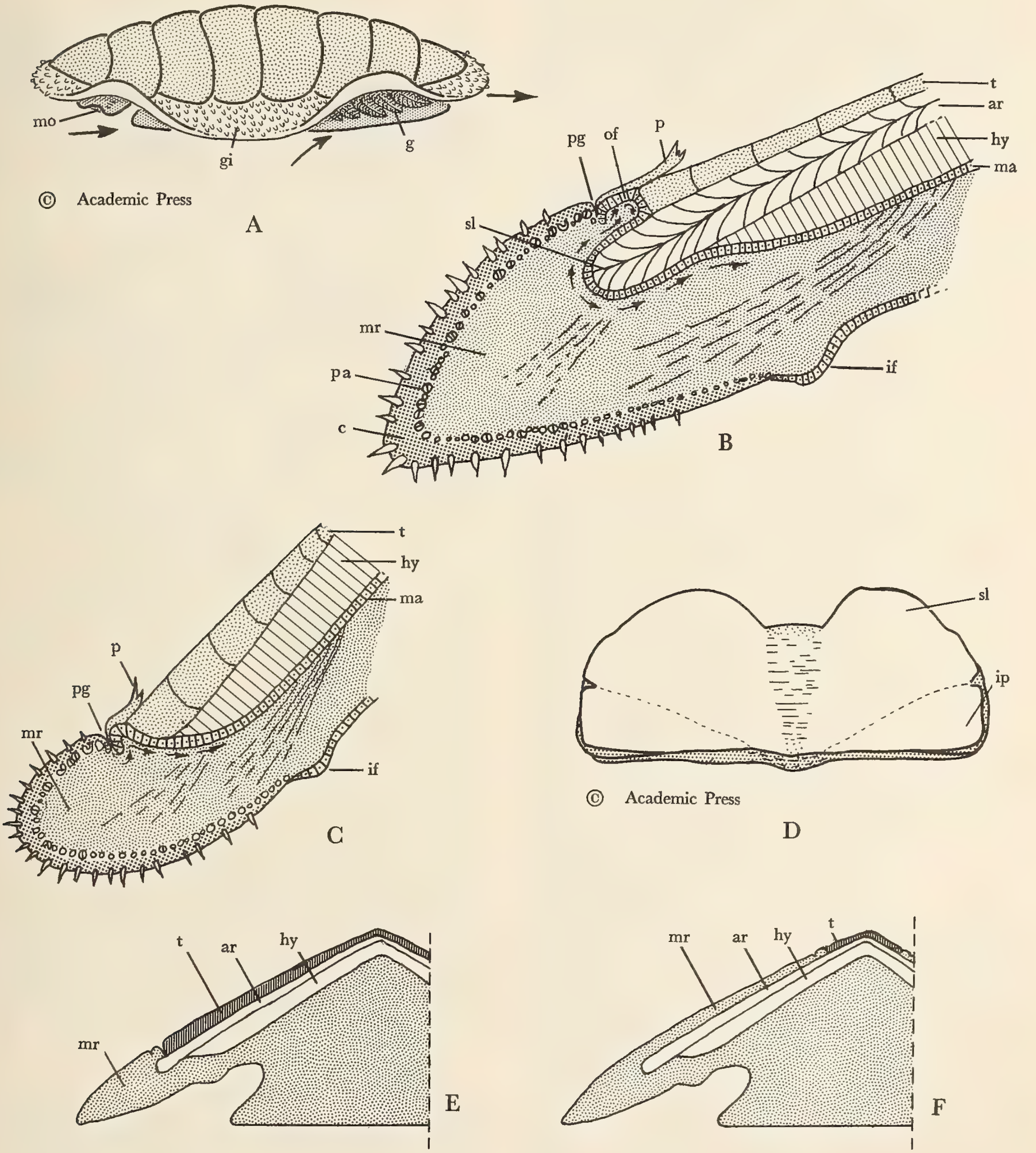
Figure 3

(on facing page →)

Polyplacophora

A. Generalized chiton from the left side showing girdle extending beyond shell plates. B. Section of shell and mantle showing enlarged mantle rim and site of periostracal groove. Small arrows suggest locations of generative zones of the mantle. C. Probable relationships of shell and mantle edge in a primitive chiton without articulamentum. D. Ventral aspect of a single valve showing structures comprising the articulamentum. E. Schematized cross-section of a chiton with extensive tegmentum. F. Schematized cross-section of a chiton with reduced tegmentum and expansive mantle covering most of the dorsal surface.

ar – articulamentum; c – cuticle; g – gill; gi – girdle; hy – hypostracum; if – inner (accessory) mantle fold; ip – insertion plate; ma – mantle; mo – mouth; mr – mantle rim (girdle); of – outer mantle fold; p – periostracum; pa – packets of epithelial cells in girdle; pg – periostracal groove; sl – sutural lamina; t – tegmentum. A and D from Stasek, 1972, © Academic Press, Inc.; B slightly modified from Stasek, 1972, based on Mutvei, 1964.



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cuticular substance. The distinctly different cell types of the mantle are demarcated by the periostracal groove.

The fossil record demonstrates that there were but two calcified shell layers in the earlier polyplacophorans (Figure 3C; Bergenhayn, 1955: 28). Differentiation of the innermost of the two primitive layers, the hypostracum (Figure 3C, hy), to form dense anterior and lateral extensions (sutural laminae and insertion plates; Figures 3B, sl; 3D, sl, ip) provided enlarged sites for muscular attachment. These extensions complicated the relationship of the shell and soft parts and comprise the third shell layer, the articulamentum (Figure 3B, ar), of modern chitons. As a specialized condition among the Acanthochitonidae and Mopaliidae, relative enlargement of the inner articulamentum and reduction of the outer tegmentum was coupled with an expansion of the girdle that may extend nearly or entirely over the entire dorsal surface of the body (Figures 3E, 3F).

The Subphylum Conchifera: The evolutionary mainstream of the phylum was determined during Precambrian times with the development of a calcified univalve shell, which was the key to the full realization of the molluscan framework as it now exists (Stasek, 1972). The most primitive univalved group to arise was the Monoplacophora, a highly diversified lower and mid-Paleozoic class with 6 or 7 living species of a single genus, *Neopilina,* having been recovered from deep water mainly in the eastern Pacific Ocean. All other higher classes of mollusks are thought to have arisen from primitive monoplacophoroids and, together with the Monoplacophora, are included in the subphylum Conchifera.

What the relationships of the mantle edge and shell may have been in the early types are unknown, but judged from the conditions in *Neopilina* and the 4 classes of mollusks considered to be descended from the Monoplacophora, there were two major kinds of association already present in the Precambrian monoplacophoroids. Transitional phylogenetic stages between the two major conditions and the ancestral condition have been illustrated in Figure 4. Of these conditions, the one typical of many gastropods (Figures 4C, 6A) and of the scaphopods (Figure 9) resembles that in the Polyplacophora and certain Aplacophora and is inferred to be primitive in that the prominent mantle rim, which may be covered by a thin cuticle (Campion, 1961), is not thrown into large folds and the periostracum is not tucked under the edge of the shell.

The second major association of the mantle edge and shell involved an undertucking of the periostracal groove beneath the mantle eaves (Figures 4D, 4E), a condition now characterizing *Neopilina* (Figure 5; Lemche & Wingstrand, 1959), the Bivalvia (Figure 10A; Yonge, 1957), and the cephalopod *Nautilus* (Figure 11A; Mutvei, 1964). This arrangement brought the mantle rim and periostracal groove under the protection of the overlying shell while permitting a more or less permanent association of the periostracal sheet with its secretory epithelium during retraction of the mantle edge. This reorientation probably arose polyphyletically among populations of Precambrian

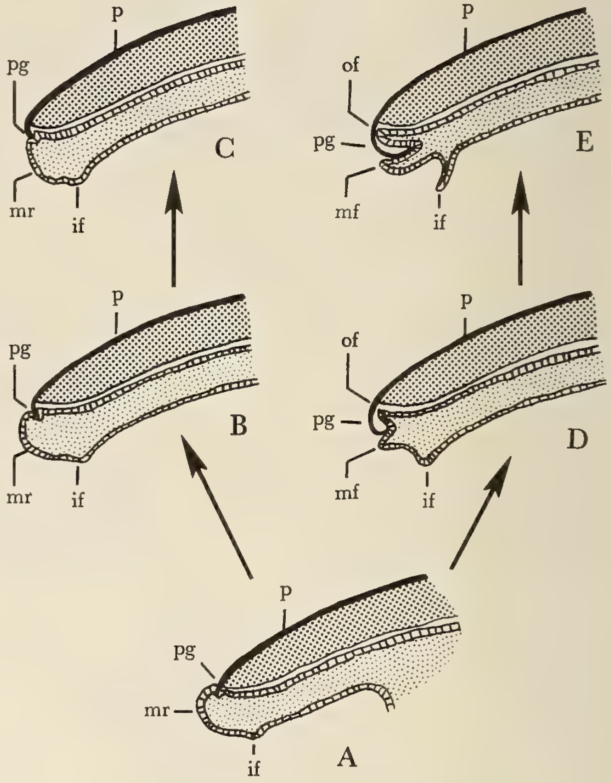


Figure 4

Phylogeny of the two major kinds of mantle edge in the Conchifera, as seen in cross-sections

A. Proposed primitive type with exposed mantle rim. Retained, perhaps, in modified form by *Haliotis,* Figure 6D. B. Transitional type with mantle rim somewhat less exposed. C. Association with periostracal groove and retractible mantle rim, the primitive condition in gastropods. D. Proposed intermediate type with a three-folded mantle edge and undertucked periostracal groove. E. Association with fully formed outer mantle fold and undertucked periostracal groove, as found in *Neopilina,* bivalves, and *Nautilus.*

if – inner mantle fold; mf – middle mantle fold (mantle rim); mr – mantle rim; of – outer mantle fold; p – periostracum; pg – periostracal groove; darker areas – calcified layers of shell.

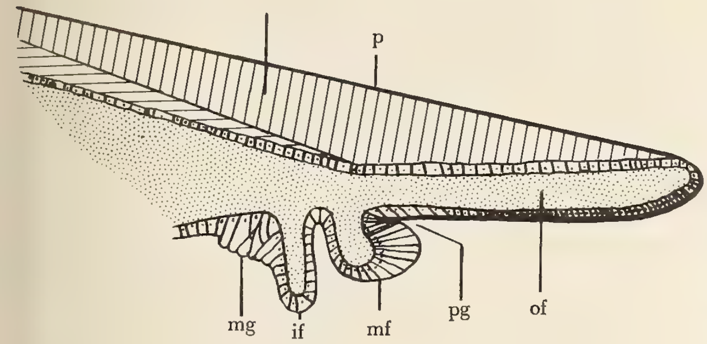


Figure 5

Neopilina

Cross-section of mantle edge showing undertucked periostracal groove and large outer mantle fold.

if – inner mantle fold; mf – middle mantle fold; mg – mucous gland; of – outer mantle fold; p – periostracum; pg – periostracal groove; sh – calcified layers of shell. Simplified from Lemche & Wingstrand, 1959, fig. 33.

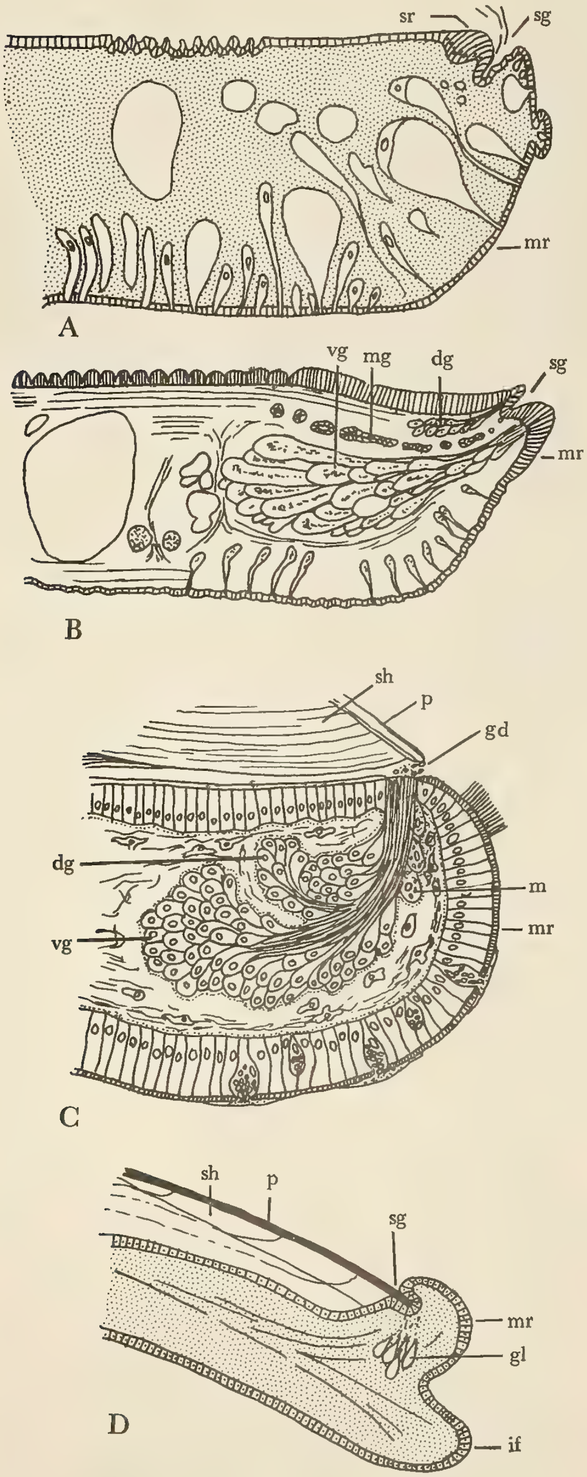
monoplacophoroids and gave rise to the state now generally regarded as typically molluscan; namely, that condition in which there is a clearly demarcated outer mantle fold (Figure 4E, of) concerned solely with secretion of the shell. The secretory ridge lying submarginally on the ventral surface of the mantle became enlarged as the inner mantle fold (Figure 4E, if), while the mantle rim, which primitively "met the environment," retained its major function of sense reception as the middle mantle fold (Figure 4E, mf).

Among gastropods, in contrast, complete protection of the mantle margin was achieved primarily through reliance upon its retraction and upon an impermanent relationship of the periostracum and its secretory epithelium. Among higher prosobranchs and many opisthobranchs a defined periostracal groove is typically lacking, and the resultant anatomical simplicity of the mantle margin could have arisen in correlation both with increased protection and with efficiency of retraction.

The Gastropoda: Among the members of this class the mantle rim is most often a simple, perhaps swollen projection in cross-section. This projection may be separated from the shell-secreting surface either by a shallow supramarginal (periostracal) groove (Figure 6A, sg), the epithelium of which may or may not be glandular in appearance; by a groove and rows of ducts issuing from large subepithelial cells (Figure 6B, vg, mg, dg); or simply by rows of ducts (Figure 6C, gd). Hyman (1967: 189) summarized information relating to the mantle margin of prosobranchs and concluded that a supramarginal groove occurs in relatively few taxa, but is found in *Haliotis* (Figure 6D) and in the Trochidae, among others. Supramarginal grooves also occur in the primitive opisthobranch *Actaeon* and among shelled pulmonates, including the primitive genus *Siphonaria* (Fretter & Graham, 1962: 130; Hyman, 1967: 554; Jones, 1935). This broad taxonomic distribution among primitive taxa suggests that while the presence of a defined periostracal groove is not necessarily common among the Gastropoda, it is a basic feature of the class and demarks the mantle rim from the supramarginal ridge (Figure 6A, sr). The absence of a groove is then to be regarded as a derived quality.

The supramarginal groove has been associated with the secretion of the periostracum, for example in the opisthobranch *Actaeon* (Perrier & Fischer, 1911) and in the pulmonate *Anguispira* (Jones, 1935). The groups of large subepithelial glands opening within or near the supramarginal groove (Figure 6B), or near the mantle margin where a groove is lacking (Figure 6C), have been interpreted as the source of periostracal material (Bevelander & Nakahara, 1970) or of shell material generally (Fisher, 1904: 36). In the limpet *Lottia* groups of glands occur at frequent intervals (Fisher, *op. cit.*). Only in very young individuals is there a continuous cordon of the glands around the mantle edge. The role of these glands was concluded to be that of shell secretion, but the evidence at present remains circumstantial, as it does in *Littorina* (Bevelander & Nakahara, *op. cit.*), for while periostracal material often can be seen emerging from the supramarginal groove where one exists, no indisputable relationship between the glandular secretions and periostracum has been demonstrated, although undoubtedly one is present.

The glandular lower surface of the mantle rim (Figures 6A, 6B, 6C) is associated with production of mucus and several other substances, including repellent or toxic secretions (Fretter & Graham, 1954; Thompson, 1960; Edmunds, 1968). Among opisthobranchs a general evolutionary trend has been towards enclosure of the shell by the reflected mantle rim and by folds of the body (Figure 7; Perrier & Fisher, 1911). The inner mantle surface so exposed bears glands that secrete noxious material (Fretter & Graham, *op. cit.;* Thompson, *op. cit.*). Increasing coverage of the shell by the tissues containing these glands, and subsequent functional replacement of the shell as a means of protection, probably explains the tendency towards reduction in the relative size of the shell in this subclass.



In a few gastropods the mantle margin is molded into folds, as in *Haliotis,* where there are two (Figure 6D), and in the fissurellid prosobranchs, for example *Diodora.* where there are three (Figure 8A). While the association of the mantle rim to the periostracal groove in *Haliotis* is clearly related to the proposed primitive state (Figure 4A) and to the widespread gastropodan condition described above, that in *Diodora* is not. Rather, the orientation of the mantle edge to the shell in that genus suggests that the upper surface of the outer of the three folds (Figure 8A, of), or perhaps its distal margin, is the site of periostracal secretion. No distinct sheet of periostracum is present; certainly none emerges from the outer of the two grooves in the mantle margin. That is, the outer groove is not a periostracal groove. We conclude, therefore, that the obviously three-folded condition of the mantle margin in the Fissurellidae is not closely related to that in bivalves described below. Instead, the complexly folded mantle edge of the fissurellids represents an independent secondary folding of the mantle rim and, in *Diodora* at least, is related to a behavioral response in the presence of echinoderms (Margolin, 1964). Upon stimulation by a seastar the middle mantle fold of *Diodora* expands up over the outer shell surface, nearly covering it, while the inner mantle fold extends downward (Figures 8B, 8C). The tube feet of the seastar seem to be unable to grasp the soft mantle tissue and to be repelled by it. The body and shell of some fissurellids, such as *Megathura,* are perma-

Figure 6

(← adjacent column)

Gastropoda

Cross-section of the mantle edge.

A. *Anguispira* (Pulmonata) with swollen mantle rim and supramarginal groove without glandular ducts entering it. Variety of subepithelial gland cells is indicated on lower mantle surface. Simplified from Jones, 1935. B. *Lottia* (Archaeogastropoda) with supramarginal groove lined by three groups of subepithelial glands. Redrawn from Fisher, 1904. C. *Littorina* (Mesogastropoda) without supramarginal groove, but with large subepithelial glands associated with secretion of periostracum. Redrawn from Bevelander & Nakahara, 1970. D. *Haliotis* (Archaeogastropoda) with supramarginal groove and glands and an enlarged inner mantle fold. Simplified from Beedham & Trueman, 1967.

dg – dorsal group of gland cells; gl – gland cells; gd – ducts of subepithelial gland cells; id – inner mantle fold; m – mucous cells; mg – median group of gland cells; mr – mantle rim; p – periostracum; sh – calcified layers of shell; sg – supramarginal groove; sr – supramarginal ridge; vg – ventral group of gland cells.

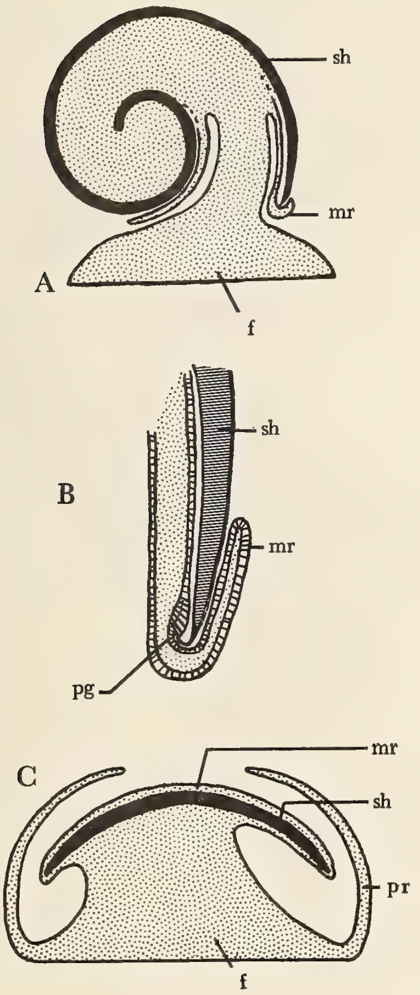


Figure 7

Enclosure of shell by the mantle in the Opisthobranchia

A. Cross-section of primitive form with large shell and mantle edge with periostracal groove. Mantle rim slightly reflected over lip of shell. Based on *Actaeon*. B. Enlarged section of mantle edge of *Actaeon*. C. Cross-section of advanced type with reduced shell enfolded by mantle rim and with parapodia extending from foot. f – foot; mr – mantle rim; pr – parapodia; sh – shell. A and B suggested by Perrier & Fischer, 1911, p. 8, fig. B, and plt. 4, fig. 8. C suggested by Lang, 1896, p. 47, fig. 56.

nently covered by overgrowth of the middle and inner mantle folds (Figures 8D, 8E; Odhner, 1932); this also is probably a defensive measure.

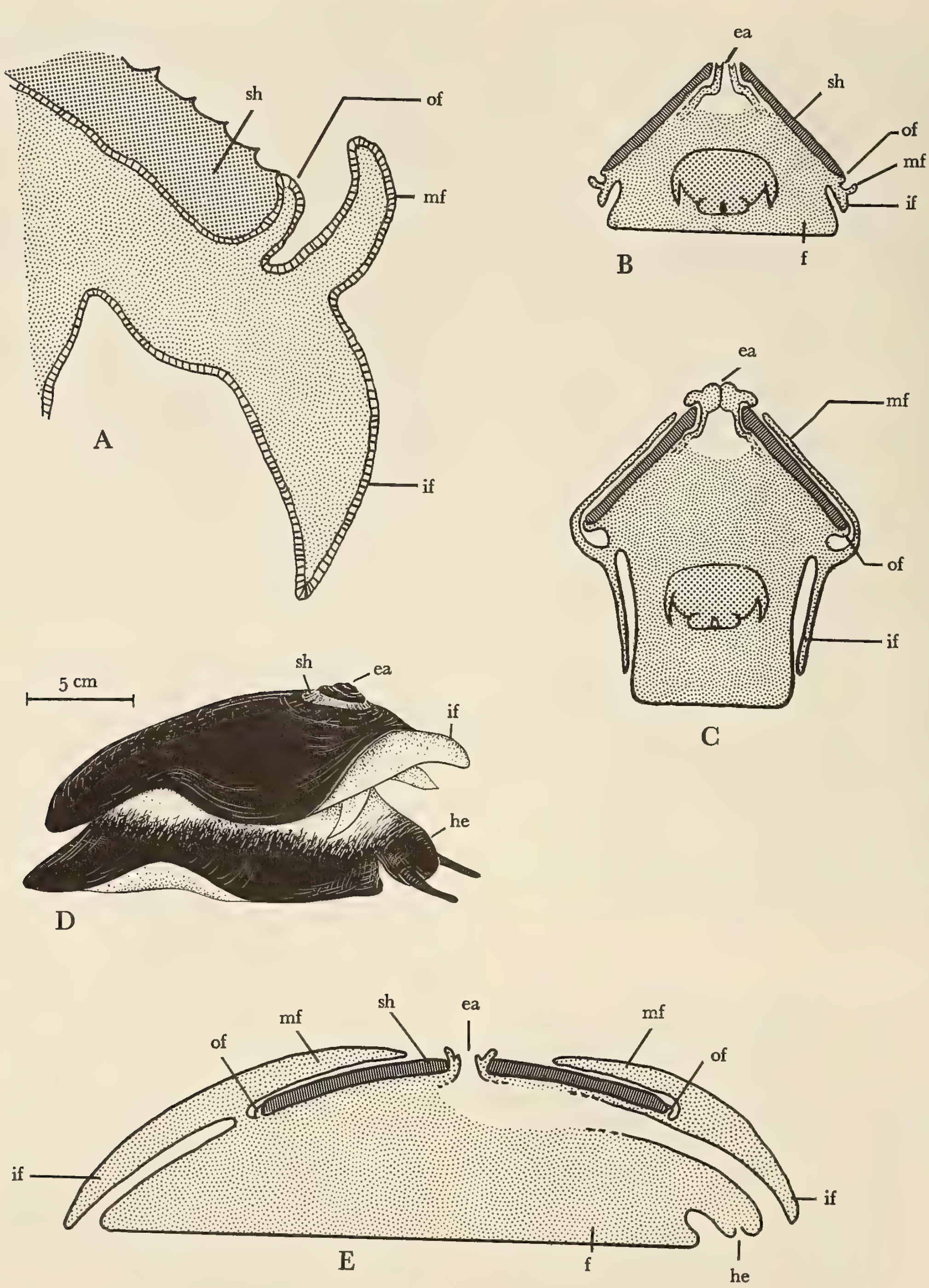
The Scaphopoda: The mantle rim at the anterior end of *Dentalium* (Figure 9A) is greatly enlarged and contains numerous flask-shaped subepithelial mucocytes on its lateral surface (Boissevain, 1904). The muscular rim is wedge-shaped in section and functions in burrowing by acting as a diaphragm around the foot, thus preventing material of the substratum from entering the anterior mantle cavity (Dinamani, 1964). Mucus, which is released in copious amounts upon the outer surface of the mantle rim, may act as a protective lubricant and has been observed by one of us (W. McW.) to bind particles of the substratum together.

The mantle edge lining the smaller, posterior opening of the shell is characterized by a modified epithelium and musculature and is termed the pavilion (Lacaze-Duthiers, 1856-1857). Flask-shaped subepithelial mucocytes resembling those of the anterior rim are present, but they are smaller and are associated with the medial, rather than the lateral surface of the mantle edge (Figure 9B). The lateral surface of the posterior mantle edge is responsible for the secretion of fragile calcareous, secondary extensions of the shell in many species (Figures 9B, 9C, ce), and may also be involved in resorptive truncation of the shell apex.

The cuboidal epithelium on either side of the shallow supramarginal groove (Figures 9A, 9B, sg) grades into a membrane so thin at the base of the groove that cells cannot be distinguished by light microscopy. Because there is no periostracum in scaphopods, the absence of secretory indications in the supramarginal groove is to be expected.

The Bivalvia: The Bivalvia have provided most of the existing information on the molluscan mantle and shell in terms of anatomy (Yonge, 1957), structure (Grégoire, 1972), mineralogy (Kennedy *et al.*, 1969), calcification (Wilbur, 1972), and shell regeneration (Beedham, 1965; Saleuddin, 1967). Because of their early prominence in investigations, the Bivalvia have supplied bases for comparisons and expectations in all of the other classes. The terms used to describe the relative conditions of the mantle margin throughout the phylum reflect this. For example, the zone of shell secretion just medial to the periostracal groove in chitons (Figure 3B, of) and gastropods (Figure 6A, sr) has been described as a reduced outer mantle fold. That this region never was prominent in either of these classes is much more likely.

Among bivalves the mantle edge is universally comprised of three basic folds (Figure 10A; Yonge, 1957), being found in members of all three subclasses: Protobranchia (Stempell, 1898), Lamellibranchia (Drew,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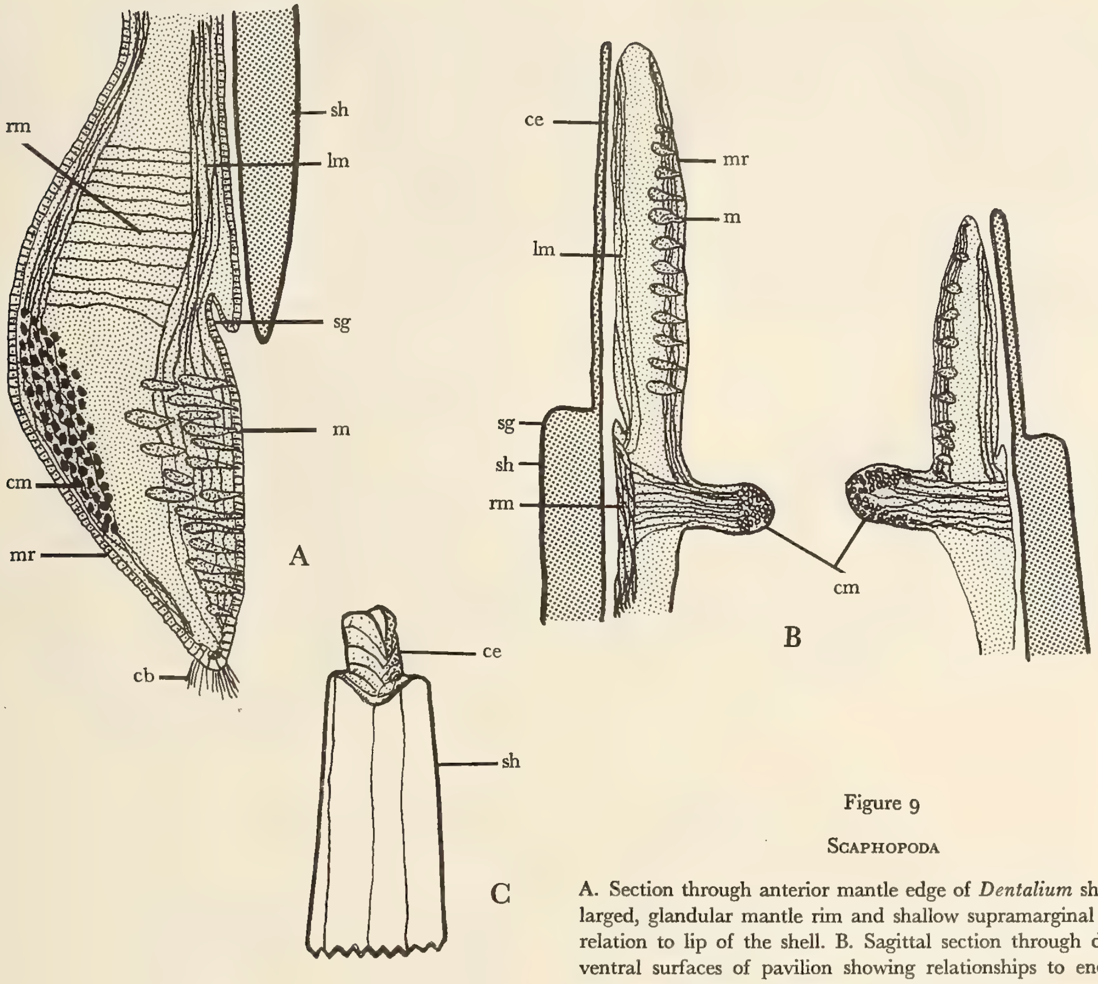


Figure 9

Scaphopoda

A. Section through anterior mantle edge of *Dentalium* showing enlarged, glandular mantle rim and shallow supramarginal groove in relation to lip of the shell. B. Sagittal section through dorsal and ventral surfaces of pavilion showing relationships to end of shell with its secondary extension. C. Posterior end of shell showing secondary extension with slit.

cb – ciliary band; ce – secondary calcareous extension at posterior end of shell; cm – circular muscles; lm – longitudinal muscles; m – mucocytes; mr – mantle rim; rm – radial muscles; sg – supramarginal groove; sh – shell.

Figure 8

(← on facing page)

Fissurellidae

A. Cross-section of mantle edge of *Diodora* showing three folds. Simplified from Fretter & Graham, 1962, fig. 80. B. Cross-section of entire *Diodora* showing relationships of shell and mantle in undisturbed state. Redrawn from Margolin, 1964. C. Relationships following stimulation by seastar. Note expanded middle fold covering the shell, and inner fold, which is extended ventrally over heightened body. Redrawn from Margolin, 1964. D. *Megathura* as seen from the right side, with anterior margin of inner fold raised revealing the gills in the mantle cavity. Adjacent to the exhalant aperture a small portion of the shell is exposed. Drawn from life by Emily Reid and included here by courtesy of Dr. R. Stohler. E. Longitudinal section of *Megathura* showing relationships of the permanently expanded fleshy inner and middle mantle folds covering the shell. Suggested by Odhner, 1932, fig. 21.

ea – exhalant aperture; f – foot; he – head; if – inner mantle fold; mf – middle mantle fold; of – outer mantle fold; sh – shell.

1906; Sullivan, 1961; Galtsoff, 1964; Saleuddin, 1967), and Septibranchia (personal observations, C. R. S.). In all of these the depression between outer and middle folds forms a periostracal groove from which the periostracum emerges, folds back around the edge of the calcareous portion of the shell, and lies appressed to its outer surface (Figure 10A). Although it is the cells of the groove and of the medial surface of the outer fold that are concerned with secretion of the layered periostracum

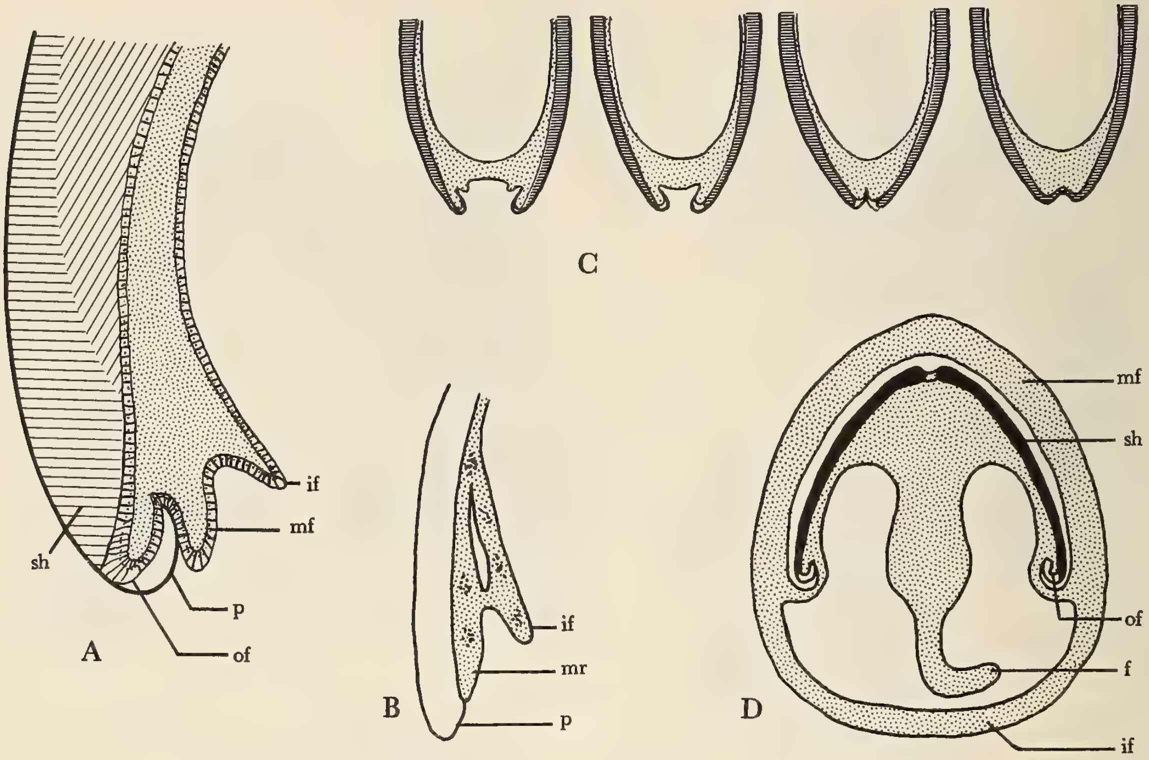


Figure 10

Bivalvia

A. Generalized cross-section of mantle edge showing three-folded nature and undertucked periostracum. Note that periostracum is adherent to lateral surface of middle mantle fold. B. Cross-section of mantle edge of metamorphosing *Venerupis* showing simple mantle rim, the periostracum arising from its margin. Simplified from Quayle, 1952, fig. 3 A. C. Various degrees of cross fusion of left and right sides of ventral mantle edges; in order, inner folds only, inner folds with medial surface of middle folds, inner and middle folds, and all three folds including the medial surfaces of outer mantle folds. From Yonge, 1957, fig. 5. D. Cross-section of a galeommatid bivalve with reduced shell completely enfolded by the middle mantle fold. Suggested by Popham, 1939, figs. 11 and 16. f – foot; if – inner mantle fold; mf – middle mantle fold; mr – mantle rim; of – outer mantle fold; p – periostracum; sh – shell.

(Bevelander & Nakahara, 1967), this material, once it is tanned, is adherent to the lateral surface of the middle fold (Figure 10A, mf). As recently as 1965, there were those who held to an older view that the latter site was responsible for elaboration of periostracal substance, at least in certain bivalves (Saleuddin, 1965: 238). A gradual distal thickening of the periostracal layer facing away from the middle fold, as indicated in Saleuddin's figure 3, suggests that this view is technically erroneous. This does not eliminate the possibility that the middle fold plays some subtle role in shell secretion (Hillman, 1969: 424).

The outer mantle fold and the deepened periostracal groove arise in bivalves from a much simpler condition during metamorphosis of the larva (Figure 10B; Meisenheimer, 1900, figures 112, 113; Drew, 1901; Quayle, 1952; Creek, 1960; Allen, 1961; Ansell, 1962). The periostracum is initially attached along the very edge of the mantle, which does not bear evidence of secretory activity or even of cell membranes between its nuclei in many instances. A submarginal fold, the future inner mantle fold, may or may not be present (*e.g., Venerupis* and *Nucula,* respectively). With further development, the more distal fold splits, resulting in two ridges, now the outer and middle mantle folds, and the periostracum emerges from the groove between them. The apparent splitting of the originally undivided mantle edge probably takes place through differential growth, although data are lacking.

Apposition of left and right sides of the mantle in this laterally compressed group has led to various degrees of fusion (Figure 10C; Yonge, 1957), and in relation to the evolution of burrowing habits, to the formation of siphons (Stanley, 1968). In such instances the three-folded nature of the mantle edge is obscured. Rarely, a fourth fold makes its appearance, as in the venerid clam *Mercenaria* (Hillman & Shuster, 1966). Histological observations suggest that the fourth fold is an elaboration combining portions of the medial surface of the third fold and of the general inner surface of the mantle surface immediately proximal to the third fold.

As in gastropods, the various regions of the bivalve mantle margin are associated with several kinds of epithelial and subepithelial secretory cells, generally mucocytes (Sullivan, 1961; Hillman, 1968), as well as others that are probably associated with calcification (Hillman, *op. cit.*) or with substances concerned with the tanning of periostracal material (Hillman, 1961).

The mantle has become highly modified in many bivalves. In relation to what is presumed to be the original function of sense reception, the middle mantle fold may bear eyes, either simple ones, as in *Cardium* (Roche, 1925) and *Tridacna* (Stasek, 1966), or complex ones, as in the Pectinidae (Dakin, 1928). Sensory tentacles also represent elaborations of the mantle rim, as in *Lima*, which, in addition, may be related to protection in that the tentacles are sticky and autotomous (Gilmour, 1967).

In relation to nutrition, it is the middle mantle fold of the siphonal regions of the giant clams that is greatly enlarged (Yonge, 1953). Symbiotic dinoflagellates housed there have been shown to release significant amounts of glycerol during metabolism, a substance that may be utilized by the bivalves as a source of energy in nutrient-poor tropical waters (Muscatine, 1967).

In certain genera of the families Galeommatidae and Montacutidae the mantle rim is reflected back over the shell, making it partially or entirely internal (Figure 10D; Popham, 1939; Judd, 1971). Reduction of the relative size of the shell is a corollary trend, suggesting that, as

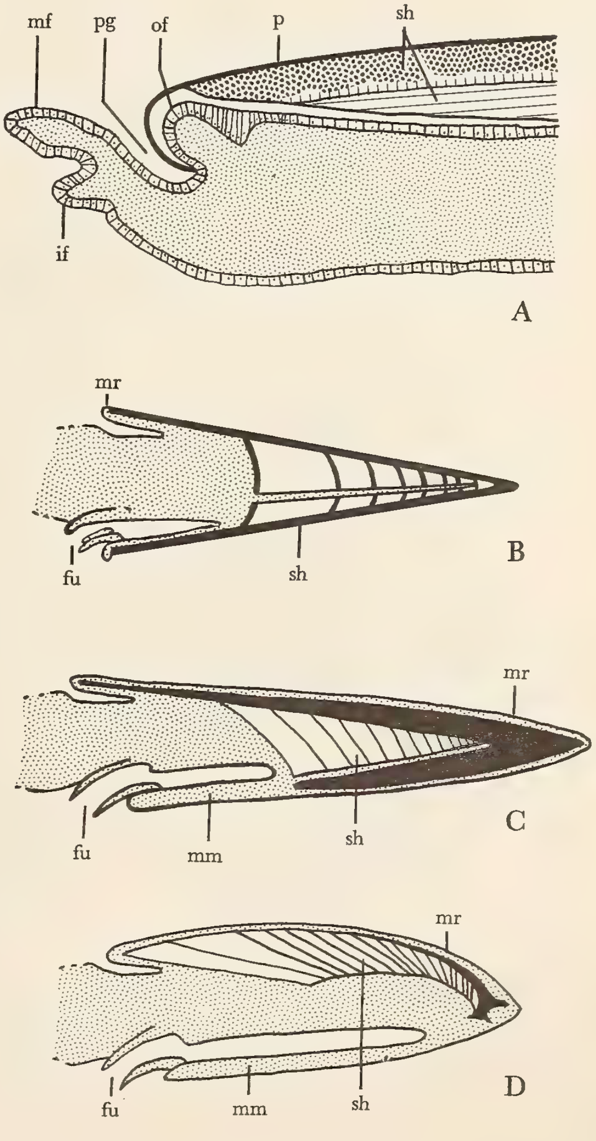


Figure 11

(adjacent column →)

Cephalopoda

A. Cross-section of mantle edge of *Nautilus* showing its three-folded nature and undertucked periostracum. B. Longitudinal section of stylized primitive nautiloid with mantle rim that terminates at lip of large, chambered shell. C. Probable relationships of extinct bellerophont showing mantle rim that has enfolded the shell, which is partially reduced ventrally in correlation with muscularization of the mantle. Secondary calcareous deposits (black) form a heavy rostrum. D. *Sepia*, the cuttlefish, showing reduced shell and rostrum (black) and muscular mantle, the rim of which covers the shell.
fu – funnel (foot); if – inner mantle fold; mf – middle mantle fold; mm – muscularized mantle; mr – mantle rim; of – outer mantle fold; p – periostracum; pg – periostracal groove; sh – shell. Trends in B, C, and D suggested by Naef, 1928, figs. 43 and 59, and Moore *et al.*, 1952, p. 344.

in the opisthobranch gastropods, an alternative defensive mechanism may be involved, although Popham (*op. cit.*: 82) related it to the commensal mode of life of these bivalves.

The inner fold generally is associated with controlling the flow of water into the mantle cavity (Yonge, 1957) and forms the muscular velum (Figure 10A, if). In relation to boring in calcareous rocks, the inner fold of the mytilid *Lithophaga* secretes an acid that etches the substratum (Yonge, 1955; Hodgkin, 1962).

The Cephalopoda: Among living cephalopods, *Nautilus* alone bears an external shell, a mantle edge with an undertucked periostracal groove, and three fairly distinct mantle folds (Figure 11A; Mutvei, 1964). Thus, in *Nautilus,* and probably in most extinct nautiloids (Figure 11B), the mantle rim terminates at the lip of the shell. The shells of all other existing cephalopods have been engulfed by overgrowth of the mantle rim (Figures 11C, 11D, mr; Naef, 1928). Reduction of the shell is again a corollary, in this instance related to increased lightening and streamlining of the body in the cuttlefish and squids, and to pumping of the muscular mantle (Figures 11C, 11D, mm), which supplies the locomotory jet force in these pelagic mollusks (Trueman & Packard, 1968). Attachments of the mantle edge to a large shell, as in the nautiloids, would not foster this mode of propulsion.

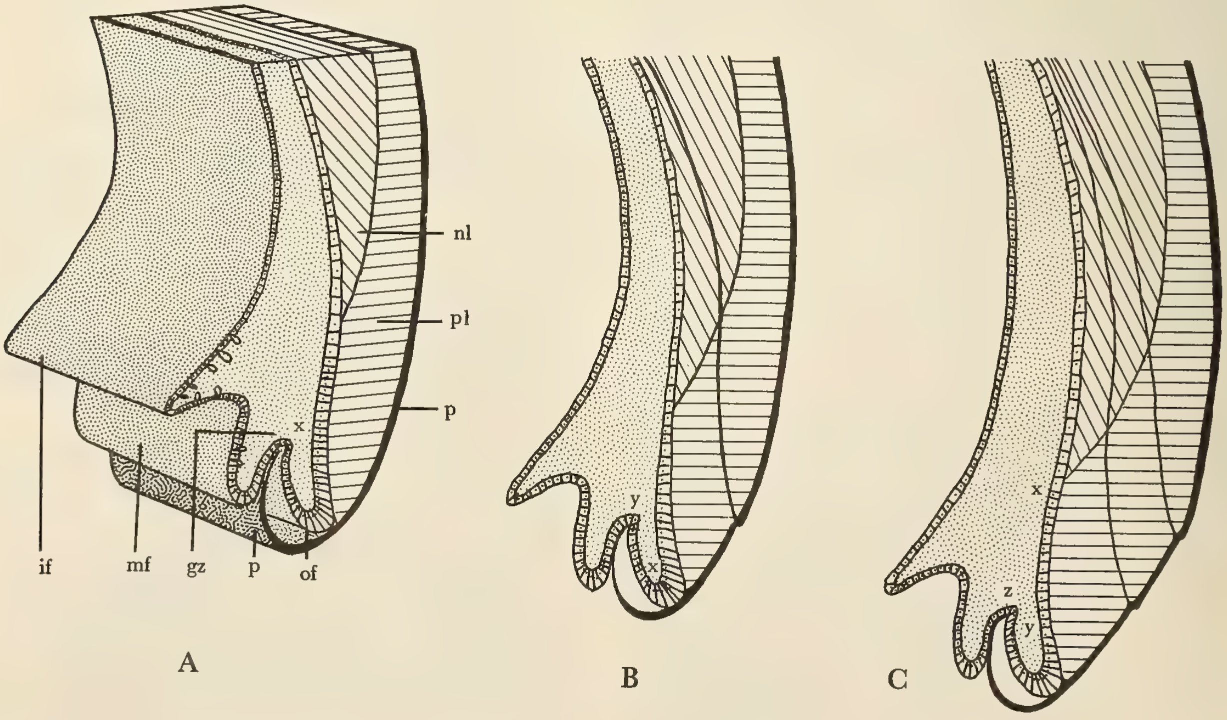


Figure 12

Generative zone of the mantle

A. Stereodiagram of mantle edge of a bivalve showing relationships of the 3 folds, periostracum, and shell layers. Cells "x" arising from depths of the outer groove produce periostracal material. B. Cross-section of same mantle edge at later growth stage (note growth line). Cells "x" have been shifted to a position at the margin of outer mantle fold by formation of cells "y". Secretory products of cells "x"has altered from periostracum to crystals of calcium carbonate in an organic matrix. That portion of periostracal sheet manufactured by cells "x" is now located at the edge of the calcified layers. C. A still later growth stage (note second growth line). Cells "x" further displaced and now secrete nacreous material. Cells "y" have been displaced by new cells "z". Cells "z" secrete periostracum, which has maintained physical continuity throughout the growth stages.

gz – generative zone of mantle; if – inner mantle fold; mf – middle mantle fold; of – outer mantle fold; p – periostracum; pl – prismatic shell layer; nl – nacreous shell layer. Suggested by Mutvei, 1964, fig. 9.

A thin cuticle covers the general epithelium of *Octopus* (Guérin, 1908) and of the cuttlefish (Fioroni, 1963) and is probably a feature of the skin of other cephalopods as well.

The GENERATIVE ZONE of the MANTLE

A ring of periostracum-secreting cells separates the mantle rim from the remaining shell-secreting surface of the mantle. In those groups with an undertucked periostracal groove the sheet of periostracum arises in the depths of the groove and bends around the edge of the shell to become appressed to its outer surface (Figure 12A). The situation is not difficult to understand if it is regarded as static, but the fact of peripheral growth confuses the issue. The way in which the periostracum is shifted in position from its site of origin to the outer shell surface, yet retains its association with the periostracal groove during enlargement of the mantle, is far from clear. Present evidence indicates the following course of events (Mutvei, 1964), which probably applies to all the Mollusca.

Cells at the bottom of the periostracal groove, or possibly first arising below the epithelium (Dunachie, 1963), are inferred to comprise a generative zone of the entire mantle. By successive divisions the cells of the generative zone push those produced earlier out onto the medial surface of the outer mantle fold, as illustrated in Figures 12A, 12B. The periostracal sheet produced by those cells is simultaneously moved or "unrolled" outwardly from the groove. During their passage, the cells enlarge and continue to have periostracal material as their secretory product. The requisite cell divisions of this process appear to be amitotic, for mitotic figures have yet to be observed (Dunachie, *op. cit.*), even in very young individuals. As stated by Cather (1967) with reference to the snail *Ilyanassa,* the cells of the mantle of metamorphosing individuals become flat and show no morphological signs of activity. The mantle edge appears to grow through incorporation of surrounding ectodermal cells, as well as through proliferation. Division figures seen in the shell gland of earlier stages never occur in differentiated mantle cells of *Ilyanassa.* That mitotic rhythms may take place was suggested by the work of Hillman (1963), who demonstrated division figures in regenerating mantle epithelium of the oyster *Crassostrea virginica.*

As the cells are displaced towards the edge of the outer mantle fold their histological appearance alters in one of several ways, and their secretory product changes from periostracum to calcium carbonate and an organic matrix upon which the calcium is deposited in crystalline (prismatic) form. The epithelial cells continue their movement and now comprise part of the outer surface of the mantle (Figures 12B, 12C). Their histological nature undergoes further changes, generally becoming lower. When the cells reach the outer submarginal region of the mantle (point "x" in Figure 12C), the crystalline material they secrete shifts from prismatic to nacreous.

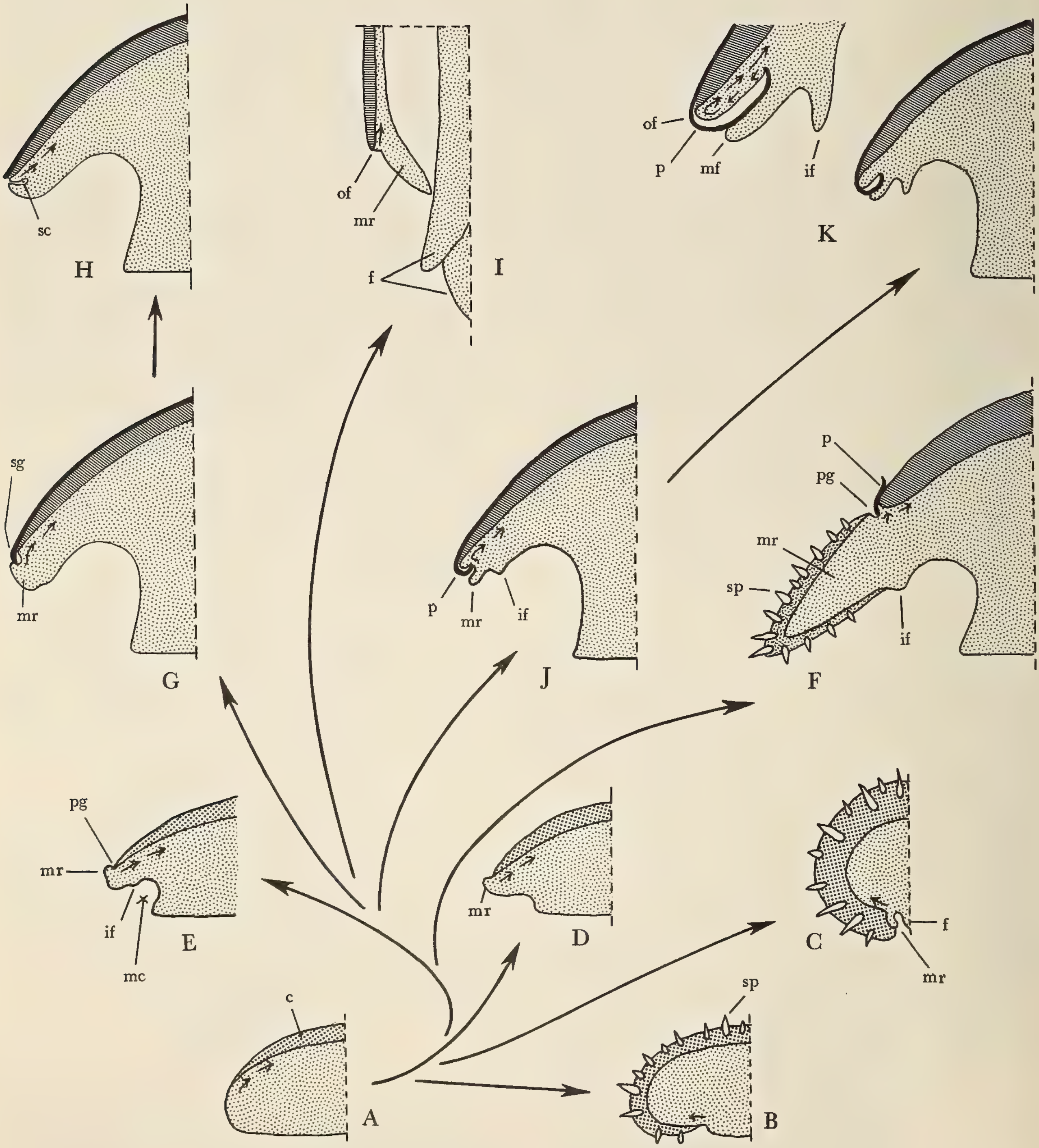
In summary, each cell originating in the generative zone of the periostracal groove is destined to be displaced by others emerging behind it and to pass over the lip of the outer mantle fold, undergoing an orderly sequence of histological and secretory modifications as it does so. The complexly layered shell is the product of this emigration with the various layers and sublayers being laid down in temporal sequence from outer to inner. Because of the unusual conformities of their valves, additional generative regions must somehow exist at the anterior edges of the sutural laminae of chitons (Figure 3B, sl; Bergenhayn, 1930; Beedham & Trueman, 1967).

The entirely circumstantial evidence for the existence of a generative zone has been summarized by Mutvei (1964). Transitional cell types between distinctive epithelial regions of the mantle edge of the gastropod *Berthelinia* (Kawaguti & Ikemoto, 1962) and the bivalves *Fabulina* and *Musculus* (Kawaguti, 1963) provide some histological evidence that in life all the cells of the mantle experience emigration from a region of proliferation and undergo gradual alterations of form as their position is shifted. A sequence of secretory and form changes is known to occur in cells located in regenerating mantle tissue of bivalves (Kawaguti, *op. cit.*; Beedham, 1965) and of the snail *Helix* (Saleuddin, 1970), although these cells in *Helix* never come to resemble those at the mantle edge.

More secure evidence for the existence of a generative zone has been found in brachiopods (Williams, 1969), so that the process has an analog elsewhere among shelled organisms. The generative zone in that phylum lies medial to the actual edge of the periostracal sheet on the undersurface of the mantle; the initial product of the cells is a mucoid substance, probably a mucopolysaccharide (Williams, 1968). The secretion of periostracum takes place under the protective cover of this material.

CONCLUSIONS

The site of periostracal secretion has been regarded in this paper as a basic landmark for the determination of homologous regions of the mantle edge throughout the Mollusca. While they, themselves, were not antecedent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to the higher classes, the variety of conditions exhibited by living Aplacophora suggests that there was a multiplicity of associations at the edge of the cuticle among the molluscan precursors (Figures 13A to 13D). The stocks characterized by only one of these associations, that in which a mantle rim and periostracal groove were developed, were successful in giving rise to advanced forms. Figure 13 depicts our interpretation of the phylogeny of the mantle edge from such an ancestor (Figure 13D). The primitive condition of the mantle margin in the early Mollusca is concluded to have been much simpler than hitherto believed. Instead of three folds, only one, the mantle rim, was at first distinct and became manifest even in a few aplacophorans (Figure 13C), but was hypertrophied as the cuticularized girdle in the chitons (Figure 13F). Cuticularization of the mantle rim also became evident in some aplacophorans, in certain gastropods, and perhaps in all cephalopods.

Among conchiferan mollusks, the basic conformities of the earlier condition have been retained by scaphopods (Figure 13I) and by most of the more primitive gastropods (Figure 13G). Active withdrawal of a simple mantle margin from the aperture of the shell, as in advanced prosobranchs (Figure 13H), or undertucking of the periostracal groove with concomitant increase in the complexity of the mantle margin combined with its withdrawal, as in bivalves (Figures 13J, 13K), represent alternative means of lending increased protection to the mantle edge.

In all likelihood, the mantle-shell associations that appeared in the phylum arose through simple variations of differential growth, as described for bivalves (p. 12) and as suggested in Figure 4. Variation in overall shell form achieved through differential growth about the periphery of the mantle, and alterations in the direction of this growth, are related aspects to be taken into account when considering success and diversity of the molluscan framework. Analyses of these geometrical attributes of shell growth have been meaningfully approached by Raup (1961, 1962, 1966, 1967), by Raup & Chamberlain (1967), and by Carter (1967). The adaptive significance of shell form has hardly been touched upon, however. The publications by Stanley (1970, 1972) and by Thayer (1972) on bivalves represent excellent and fruitful approaches to this topic.

The mantle, especially the mantle rim, has folded back over the shell in several taxa, including representatives of the Polyplacophora (Acanthochitonidae), the Gastropoda (Fissurellidae, Opisthobranchia), the Bivalvia (Galeommatidae, Montacutidae), and the Cephalopoda (Coleoidea). Generally, there is corresponding reduction of the shell in these forms. The adaptive significance of enfoldment has been fairly treated in the literature only for the gastropods and cephalopods.

The "unrolling" of the shell-secreting epithelium from a generative zone of the mantle and the temporal sequence of secretory activity undergone by the cells as they emigrate out of the periostracal groove, or its equivalent where a groove is absent, are inferred to have been related to the early selection of the successful molluscan stem-groups in that these processes led not only to the evolution of an organized calcified shell that grew by peripheral accretion, but provided a mechanism that permitted evolutionary size increases while lending a means of protection to the soft parts regardless of their size. Trends towards larger size from relatively tiny ancestral forms characterize all of the higher molluscan classes (Stasek, 1972: 11). The mechanism underlying accretionary shell growth, combined with the tendencies towards larger size fostered by this mechanism, were factors of paramount importance in severing the ties with the original turbellariform groundplan and in establishing the Mollusca as a significant phylum.

Figure 13

(← on facing page)

Phylogeny of the mantle edge in the Mollusca, as seen in cross-sections.

A. Cuticularized turbellariform ancestor. B. Proposed spiculose intermediate type related to the Aplacophora without pedal folds or mantle rim (Figure 2D). C. Aplacophora with single pedal fold (mantle rim) and narrow foot. D. Proposed ancestral condition in which a mantle rim projects beyond the margin of the cuticle. An incipient periostracal groove is present. E. A more advanced type with deeper mantle cavity and possibly lacking calcified shell layers. E. Polyplacophora with enlarged, cuticularized, and spiculose mantle rim (girdle). Calcified layers laid down under transient periostracum. G. Primitive condition in gastropods with projecting mantle rim and a supramarginal groove. H. Advanced condition in gastropods without supramarginal groove. I. Scaphopoda with enlarged mantle rim acting as a diaphragm around the foot. J. Proposed intermediate form with partially undertucked periostracal groove and enlarged inner mantle fold. K. Generalized cross-section and enlargement of the probably convergent condition in *Neopilina,* bivalves and *Nautilus,* all with well formed outer mantle fold and undertucked periostracal groove. c – cuticle; f – foot; if – inner mantle fold; mc – mantle cavity; mr – mantle rim; of – outer mantle fold; p – periostracum; pg – periostracal groove; sc – subepithelial secretory cells; sg – supramarginal groove; sp – spicules; calcified layers of shell are darker, uncalcified cuticle lighter. Small arrows suggest probable directions taken by cells from generative zones of the mantle.

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